THE ANATOMICAL RECORD, VOL. 17, NO. 2
OCTOBER, 1919

Resumen por el autor, Edward Phelps Allis, Jr.

Sobre las homologías del hueso escamoso de los peces.

El pterótico (escamoso) y el esfenótico de los peces se desarrollan en posición dorsomesial con referencia a la cresta del canal semicircular lateral, y desde este sitio se extienden mesialm nte hacia el frontal y el parietal. Ambos huesos pueden adquirir relaciones primarias con el cartílago subyacente y pueden entonces encerrar, entre las placas externas e internas, un espacio que, cuando es invadido posteriormente por los músculos del tronco, se transforma en la fosa temporal de los peces. En todos los vertebrados superiores este espacio es invadido por el músculo temporal y se transforma en una parte de la fosa temporal de los mamíferos. La porción cerebral de la escama del hombre y el proceso zigomático se derivan solamente del esfenótico de los peces o de este hueso fusionado con el pterótico. La parte auricular de la escama se forma por la placa de la mejilla de los peces. El timpánico de los mamiferos y el cuadrado-yugal de los anficios y reptiles se derivan del preopérculo de los peces. El yugal se forma por la fusión de algunos de los huesos suborbitarios y postorbitarios de los peces fusionándose con el maxilar de estos para formar el maxilar de los mamíferos. El malar es el postorbitario dorsal de los peces. Las combinaciones de estos diferentes huesos originan cuatro arcos temporales esencialmente diferentes: uno formado por el dermoesfenótico y el postorbitario de los peces (hombre) otro por la placa de la mejilla y el postorbitario o yugal (saurios); otro por el cuadradoyugal y el yugal (arco infratemporal de los reptiles) y finalmente otro arco constituido por el cuadradoyugal y el maxilar de los peces (arco infratemporal de los anfibios).

Translation by José F. Nonidez
Carnegie Institution of Washington

ON THE HOMOLOGIES OF THE SQUAMOSAL BONE OF FISHES

EDWARD PHELPS ALLIS, JR

Menton, France

The squamosal of fishes, frequently called the pterotic by English authors, is primarily a dermal bone which develops along the dorsal surface of the ridge of the lateral semicircular canal and encloses a section of the main infraorbital latero-sensory canal that is innervated in part by a prespiracular nerve and in part by a postspiracular one. As the bone develops it extends mesially and, bridging the supraotic depression, articulates either with the parietal alone or with that bone and the frontal. Anteriorly it articulates either with the frontal or the postfrontal, or with both those bones. This is the primitive condition of the bone, and occurs in the recent Holostei and Crossopterygii, the bone in the latter fishes (Polypterus) being fused with the parietal to form the squamosoparietal of van Wijhe's ('82) descriptions. In the Teleostei the primarily wholly dermal bone usually acquires primary relations to the chondrocranium, and may then be composed of external and internal plates, both of which project mesially from the lateral portion of the bone, one in the roof and the other in the floor of the piscine temporal fossa, one or both of them reaching and articulating with the parietal. The lateral surface of the bone usually forms part of the dorsal boundary of the articular facet for the hyomandibula, and dorsal to that facet it gives movable articulation to the bones of the cheek.

The postfrontal is difficult to define, and even to identify, and there is, as will later appear, much question as to its homologue in higher vertebrates. In Amia, where it occurs in what is considered to be a primitive condition, it is a dermal bone lying along the lateral edge of the hind end of the frontal, with

its own hind end lying on the dorsal surface of the postorbital process of the chondrocranium and there articulating with the anterior end of the dermopterotic. The summit of the postorbital process ossifies as the sphenotic of English authors, and the postfrontal, because of its relations to that bone, is frequently called the dermosphenotic, and, to avoid confusion, I shall hereafter so refer to it. It is traversed by the main infraorbital laterosensory canal and lodges the organ of that line that lies next anterior to the point where the infraorbital and supraorbital canals anastomose with each other, that anastomosis taking place along the mesial edge of the dermosphenotic, between it and the frontal (Allis, '89). The bone of Amia does not fuse with the underlying autosphenotic, nor does it, so far as I know, in any of the Holostei and Toleostei. In Polypterus it is completely fused with the antosphenotic even in a 75-mm. specimen, and the conditions indicate that two independent ossifications at no time here existed, a primarily purely dermal bone simply acquiring primary relations to the underlying cartilage.

I formerly considered the most definite characteristic of this bone of fishes to be the laterosensory organ that it lodges (Allis, '04), but as so identified the bone varies greatly in its relations to the other bones of the region, and also to the orbit, this apparently being definitely related to the length of the interval between the orbit (external opening of the orbital fossa) and the postorbital process. In Polypterus, where this interval is large, the dermosphenotic lies directly anterior to the dermopterotic and only reaches the hind end of the postorbital, thus forming no part of the boundary of the orbit. In Amia, where the interval is less large, the bone also lies directly anterior to the pterotic, but its anterior end here reaches to, and forms part of the boundary of the orbit. In those of the Teleostei in which the orbit is large and reaches nearly to the transverse plane of the postorbital process, the bone, as identified by the laterosensory organ it lodges, may be reduced to a small ossicle, may be pushed ventrally and become the dorsal one of the postorbital bones, or, as in Hydrocyon and Alestes, be pushed dorso-an-

teriorly and become the posterior one of a supra-orbital series (Allis, '04). When the bone lies directly anterior to the dermopterotic it forms the anterior portion of the articular joint for the bones of the cheek, but when it has a postorbital position, it, itself, articulates with the frontal and dermopterotic.

In Rhizodopsis sauroides there are two bones which together have the position of the single dermopterotic of Amia, and they are called by Traquair ('81) the squamosal and postfrontal. The postfrontal articulates anteriorly with the lateral portion of the hind end of the frontal, that portion of the frontal having the general relations to the orbit and the dorsal postorbital bone that the dermosphenotic (postfrontal) of Amia has. The so-called postfrontal of Rhizodopsis does not reach the orbit, and its position is such that the main infra-orbital laterosensory canal could not pass from it into the dorsal postorbital without traversing the lateroposterior corner of the frontal. This bone of Rhizodopsis is nevertheless said by Traquair to be the homologue of the similarly named bone of Amia (my dermosphenotic), which does reach the orbit. The corresponding bone of the Palaeoniscidae is said by Traquair to be placed still farther forward, because of the greater proportional length of the squamosal (dermopterotic), and his figure of Nematopychius ('77) shows that it may even become a definitely supra-orbital bone. Whether or not this bone of the Palaeoniscidae is traversed by the main infraorbital canal is not stated, but as the similarly placed bone of both Hydrocyon and Alestes is traversed by that canal, it would seem as if the bone of the Palaeoniscidae must also be.

In Osteolepis macrolepidotus there are two bones which correspond strictly in position to the so-called squamosal and postfrontal of Rhizodopsis, but they are called by Goodrich ('19) the supratemporal and intertemporal. They are evidently the homologues of the two bones of Rhizodopsis, and they apparently correspond, respectively, to the posterior and anterior portions of the dermopterotic of Amia; the one doubtless representing that part of the bone of Amia that lodges that part of the laterosensory canal that is innervated by the supratemporal

branch of the glossopharyngeus, and the other the part innervated by the ramus oticus lateralis. Anterior to them there is a bone, called by Goodrich the postfrontal, which has the position of that bone (dermosphenotic) of Amia, and the infra-orbital and supra-orbital canals are said to anastomose with each other in it. It articulates anteriorly with a supraorbital bone, resembling in this the dermosphenotics of Hydrocyon and Alestes, and although it is unusual for the infra-orbital and supra-orbital canals to anastomose with each other in this bone of recent fishes, it is nevertheless probably that bone.

Osteolepis thus, in so far as the bones here under consideration are concerned, strikingly resembles Amia, but Glyptopomus kinnairdi, which is also one of the Osteolepidae, just as strikingly resembles Polypterus. Like the latter fish, Glyptopomus is greatly elongated and has a small orbit placed far forward. Lateral to the parietal there are two bones which are called by Watson and Day ('16) the supratemporal and intertemporal, and they have exactly the positions of the similarly named bones of Osteolepis and also of the pterotic portion of the squamoso-parietal of Polypterus. Anterior to them, along the lateral edge of the hind end of the frontal, there is a narrow so-called postfrontal which has exactly the position of the dermosphenotic of Polypterus, and seems unquestionably to be the homologue of that bone. Comparison with Rhizodopsis would then confirm my conclusion that the dermosphenotic of that fish has fused with the frontal, if it be not that the bone, which is inconspicuous in Polypterus, has simply been overlooked. Ventro-lateral to it and the frontal there is, in Glyptopomus, a long postorbital, which, with the jugal, forms the posterior boundary of the orbit.

There are two cheek-plates in Rhizodopsis, one dorsal to the other. The dorsal one and the preoperculum, together, are said by Traquair to correspond to the large cheek-plate of his descriptions ('70) of Polypterus. The ventral one lies immediately above the articular extremity of the mandible and external to the ventral end of the preoperculum, and Traquair considers it to be the homologue of the bone y'' of his descriptions of Polyp-

terus. In both Osteolepis and Glyptopomus these two cheek-plates of Rhizodopsis have fused to form a single bone, and it is called by both Goodrich and Watson and Day the squamosal. In Polypterus the two bones have fused with each other and also with the preoperculum, while in Amia they remain separate and are represented in the posterior portions of the two postorbitals. The cheek-plate lies external to the adductor mandibulae and dilatator operculi muscles, and external also to the trigeminofacialis chamber, the lateral wall of that chamber being formed by the posterior branchial-ray bar of the mandibular arch (Allis, '18).

The names given by Goodrich and Watson and Day to the bones above referred to in Osteolepis and Glyptopomus are those recently adopted by a Committee of the American Paleontological Society (Gregory, '17) for certain of the cranial bones of the Tetrapoda, and their use by these authors indicates that they consider the bones of these fishes to be the homologues of the similarly named ones of the Tetrapoda. The cheek-plate of fishes thus becomes the homologue of the squamosal of mammals. That this bone of fishes might become the zygomatic process of the squamosal of mammals is possible, but that it could become the squamous portion of the temporal bone of man, which lies internal to the temporalis muscle, seems to me wholly impossible. My views regarding it can be best presented by considering the conditions in Polypterus.

In Polypterus the musculus adductor mandibulae has been differentiated into masseter, temporalis, and pterygoideus portions (Pollard, '92). The masseter portion arises mainly from the external surface of the suspensorial apparatus, but partly also from the internal surface of the dorsal margin of the large cheek-plate. Its surface of origin lies wholly posterior to the postorbital process of the chondrocranium, and the muscle is covered externally by the cheek-plate. The temporalis runs upward anterior to the postorbital process, and having worn through the cartilaginous roof of the posterior portion of the orbital fossa, has its origin on the ventral surface of the frontal. The muscle occupies the posterior two-thirds of the greatly

elongated orbital fossa, this portion of the fossa thus corresponding, in this respect, to the ventral portion of the temporal fossa of man. The sphenotic, formed by the fusion of the dermosphenotic and autosphenotic, has a long anterior process which projects forward along the external surface of the temporalis, and, articulating with the postorbital bone, forms a supratemporal arch.

Assume that, in a vertebrate in which the conditions were as above set forth in Polypterus, the postorbital process of the chondrocranium were to be retarded in development, or to actually diminish in relative importance, as is actually the case in the Amphibia and Reptilia (Allis, in press). The musculus temporalis would then naturally push posteriorly beneath the frontal and the dermopterotic, but external to the primary (substituent) portions of the sphenotic and pterotic, if present, and would necessarily enter the supra-otic depression on the dorsal surface of the otic capsule; and this is exactly the position that the posterior portion of this muscle has in embryos of both Hatteria and Chelone (Fuchs, '11; figs. 31 to 38). This invasion of the supra-otic depression by a muscle is not exceptional, for it is so invaded in Amia and many of the Teleostei, the invasion there, however, being, either from the side by the masseter or from behind by the trunk muscles. The latter invasion gives origin to the piscine temporal fossa, and when the pterotic has primary relations to the chondrocranium, as in the Teleostei, the dermopterotic tends to become less strongly developed, and may almost entirely disappear, the primarily closed temporal fossa then becoming a more or less open groove on the dorsal surface of the cranium. If similar reduction, first of the pterotic and then of the sphenotic and frontal, were to take place in a vertebrate in which the supra-otic depression had been invaded by the musculus temporalis, it would first give rise to the small supratemporal fenestra of the Crocodilia and then to the larger one of man. If the supra-otic depression were to open posteriorly on to the posterior surface of the cranium by passing internal to the dermopterotic, and internal also to the extrascapula (supratemporal) if it persisted, as the piscine temporal fossa

does in Amia, a posttemporal arch would be formed similar to that in Hatteria. If this arch were to disappear, it would give rise to the conditions in Testudo tabulata (Gaupp, '94, fig. 3); and if, in addition, the supratemporal arch were to disappear, the conditions in Cistudo would arise. Williston's ('04) conclusion that the large fossa of the Testudinata is not a supratemporal fossa would thus seem incorrect, for the fossa of these reptiles has the same relations to the otic capsule that it has in Crocodilus and Hatteria, lodges the same muscle, and is bounded by the same bones. The roof of the fossa may have here disappeared as the result of emargination from behind, as Williston suggests, but this would not affect the homologies of the fossa.

That the temporal fossa must have been thus developed from conditions similar to those in Polypterus seems almost self-evident, and if so the bounding and related bones should be homologous. Comparison is most easily first made with man. In man the fossa lodges the musculus temporalis in its dorsal portion, and that muscle and the pterygoideus in its ventral portion, as it does in Polypterus. The inner aspect of the squama of man has (Bryce, '15) cerebral and aural parts separated by a projecting ridge (crista petrosa) which articulates with the outer edge of the tegmen tympani. The so-called tegmen tympani of mammalian embryos is a cartilaginous ridge which corresponds to the sphenotic portion of the sphenopterotic ridge of fishes (Allis, in press), and as the crista petrosa articulates with it, that crista is a ridge along the internal surface of the lateral edge of the dermosphenotic of fishes. The aural part of the squama lies morphologically ventral to the crista petrosa, forms the outer wall of the recessus epitympanicus and the antrum mastoideum, and lies external to the incus and the tensor tympani. The incus is derived, if I am correct in my recent conclusions (Allis, in press), from the posterior branchial-ray bar of the mandibular arch, and is the homologue of the lateral wall of the trigeminofacialis chamber of fishes; and the tensor tympani would seem to have certainly been derived from the dilatator operculi of fishes, for the two muscles have similar relations to the cheek-plate and are both innervated by the nervus

trigeminus. The masseter, which in Polypterus arises from the outer surface of the suspensorial apparatus and the inner surface of the dorsal margin of the cheek-plate, arises, in man, from the zygomatic process, an origin which would be naturally acquired as the hyomandibula and quadrate became functionally related to the ear. The aural part of the squama thus has exactly the topographical position and relations of the cheek-plate of fishes, and as this bone of fishes frequently fuses with adjacent bones, it seems certain that it has here fused with the sphenotic. The cerebral part of the squama and the zygomatic process are then both parts of the sphenotic of fishes, the zygomatic process apparently representing the dermal component of that bone as found in Polypterus, and the cerebral part of the squama being either the autosphenotic, ossified in membrane that represents an unchondrified portion of the postorbital process, or being an internal plate of the dermosphenotic, not found in fishes, which has developed, as shown in Fuchs's figure ('11, fig. 38) of Chelone, internal to the temporalis, along the outer surface of the chondrocranium, and there replaced the mesial limb of the autosphenotic. In favor of the latter supposition is Bryce's (l.c., p. 72) statement that: "According to Sutton the tegmen tympani is the seat of a separate centre (pterotic), which extends from the superior and over the lateral semicircular canal, and encloses the tympanic part of the facial canal." The cerebral part of the squama thus has to this so-called pterotic center of ossification the relations that the dermosphenotic of fishes has to the autosphenotic, and it is exceedingly probable that these two ossifications of the skull of man are the homologues of the two bones of fishes. If this be so, the autopterotic of fishes is either absent in man, as it is in Polypterus, or has fused with the autosphenotic; and the dermopterotic must also either be absent or be fused with either the dermosphenotic or the parietal.

In the Reptilia and Amphibia the conditions differ somewhat from those above described.

In early embryos of Hatteria (Schauinsland, '03; Fuchs, '11) the lateral edge of the so-called squamosal lies along the outer

surface of the ridge of the lateral semicircular canal, slightly overlapping the dorsal edge of the quadrate. From there the squamosal projects dorsomesially across the supraotic depression, and its posterior portion acquires articulation with the parietal. The supraotic depression lodges the musculus temporalis. In later stages of development the squamosal sends a process anteriorly, approximately in the line prolonged of the ridge of the lateral semicircular canal, and, acquiring contact with the hind end of the postorbital, forms the supratemporal arch. A second process is sent ventrally along the external surface of the quadrate, and, passing external to the anterior edge of the quadratojugal, acquires contact with the hind end of the jugal, thus forming, with the two latter bones, the infratemporal arch. The internal plate of the bone, said by Fuchs to develop later than the external one and to form the floor of the temporal fossa, replaces the mesial limbs of the autosphenotic and autopterotic, one or both, of fishes. The jugal is formed by the fusion of certain of the suborbital and postorbital bones of fishes.

The squamosal of Hatteria thus markedly resembles the sphenotic and pterotic, combined, of Polypterus, fused with the cheek-plate of that fish. There in no indication, in the ontogenetic development of this reptile, that the squamosal has been formed by the fusion of two primarily independent bones, but this does not definitely establish that it was not so represented phylogenetically. Baur is said to have considered it to be formed by the fusion of the squamosal and prosquamosal of certain other reptiles, which bones are the pterotic and cheek-plate of fishes. Whether or not the prosquamosal of these reptiles contained some part of the preoperculum of fishes, as the cheek-plate of Polypterus does, is not indicated.

The preoperculum of fishes is quite certainly formed, phylogenetically, by the fusion of several primarily independent laterosensory ossicles, and as it is extensively present in fishes, it seems improbable that it has wholly disappeared in higher vertebrates. Its dorsal end is attached to the hyomandibula, but its ventral end may be attached to the quadrate, the bone

then extending from the hyal to the mandibular arch, across the ventral end of the spiracular cleft. In both the Reptilia and Amphibia the hyomandibula becomes functionally related to the ear. The dorsal end of the preoperculum would consequently lose its underlying support, and hence be obliged either to acquire other support, to undergo functional modification, or to disappear. When, in mammals, the quadrate also became functionally related to the ear, the preoperculum apparently became the tympanic, that bone hence naturally forming the ventral boundary of the persisting remnant of the spiracular cleft. In reptiles, where the quadrate persists, the ventral portion of the preoperculum has shifted forward on to the external surface of that element and become the quadratojugal. The dorsal portion of the bone has probably here wholly disappeared, but the cheek-plate, which is related to it, and in Polypterus fused with it, seems certainly to have persisted, as it has in man, and, acquiring attachment to the quadrate, become the ventral process of the squamosal.

The postfrontal of Hatteria lies dorsal to the postorbital, between it and the frontal and parietal, and widely separated from both the squamosal and the otic capsule, and it is apparently the homologue of the postfrontal of the Stegocephali. The bone in the latter vertebrates has somewhat the position of the postfrontal of Hydrocyon and Alestes, but it is, in all of the several species figured by Moodie ('08), definitely related to the groove of the supra-orbital laterosensory line and not to that of the infra-orbital one. The infra-orbital groove varies somewhat in general position and in its relations to the cranial bones. In a diagram given by Moodie and said to represent all of the grooves that occur on the crania of the Stegocephali, the infra-orbital groove passes from the postorbital on to the frontal and then on to the so-called squamosal of his descriptions, but in the figures given of Anachisma, Metoposaurus, and Trematosaurus, it passes from the postorbital directly on to the so-called squamosal. In both Anachisma and Metoposaurus it is interrupted as it crosses the latter bone, this interruption evidently indicating that that part of the laterosensory line that is related to this

bone was innervated, as it is in fishes, in part by a prespiracular nerve and in part by a postspiracular one. The parts so innervated apparently correspond to the intertemporal and supratemporal of Fuchs's ('10) figure of what he calls the skull of a primitive species of these vertebrates, and the intertemporal part of the bone articulates anteriorly with both the postfrontal and the postorbital. The infraorbital groove runs forward, as above stated, on to the postorbital without coming into any relation whatever to the postfrontal.

There accordingly is question as to which bone of the Stegocephali corresponds to the dermosphenotic (postfrontal) of fishes. If the laterosensory lines are here of any value in establishing the homologies of the related bones, the dermosphenotic of fishes cannot either be, or be included in, the postfrontal of the Stegocephali, and it must accordingly be either the intertemporal or the postorbital, or be included in one of those two bones, and the fact that the infra-orbital and supra-orbital grooves anastomose with each other in the postorbital in both Anachisma and Mastodonsaurus favors the view that that bone is the homologue of the postfrontal of Osteolepis, and hence probably a dermosphenotic. It must, however, be borne in mind that the laterosensory lines of the Stegocephali were probably lines of pit organs, and hence presumably less fixed in their relations to the underlying bones than the canal lines of fishes are. The postfrontal of these vertebrates may accordingly be a dermosphenotic, notwithstanding its different relations to the laterosensory lines. The postfrontal of the Reptilia, however, lies so far in front of the otic capsule that it would seem as if it could not be a dermosphenotic, and if this be so, the latter bone must be either included in the intertemporal or the postorbital, or be represented by one of those two bones, and comparison with Polypterus and Glyptopomus would seem to indicate that it is included in the intertemporal, and hence in the squamosal of Hatteria.

In the Reptilia the maxillary is apparently of the mammalian type, and, as already stated, certain of the suborbital and postorbital bones have fused to form the jugal. The inferior tem-

poral arch of Hatteria has accordingly been formed by the cheek-plate and preoperculum of fishes, posteriorly, and the suborbital and postorbital bones anteriorly; and the superior arch by the sphenotic and pterotic, one or both, and the dorsal postorbital. In the Amphibia and Stegocephali the maxillary is certainly frequently of the piscine type, and the quadratojugal (preoperculum) has accordingly here acquired contact with the hind end of the maxillary, possibly with the intermediation of the bone y″ of Polypterus, and so formed the inferior arch of these vertebrates, which thus, as is generally accepted, is not the homologue of the inferior arch of the Reptilia.

In Crocodilus (Shiino, '14) the squamosal (sphenopterotic) is similar to that in Hatteria, but its ventral process is less long. In Chelone the quadrate has either grown or shifted upward, and in embryos its dorsal edge lies dorsal to the ridge of the lateral semicircular canal (Fuchs, '11, and Kunkel, '11). The squamosal of this reptile has accordingly been forced away from the otic capsule and has, in embryos, no direct relations to it. Whether the cheek-plate has fused with this bone or with the quadratojugal is uncertain. Williston ('04) concluded that, if present, it had fused with the quadratojugal.

In the Sauria the conditions are somewhat different from those above considered. Here, in both lacerta (Gaupp, '94) and Scleroporus (Thyng, '06), a bone develops in exactly the general position of the squamosal of Hatteria and Crocodilus, but neither anterior nor ventral processes are later developed. This bone was first called by Gaupp the squamosal, but later ('10; p. 416) the supratemporal; but whether he intended, by this choice of name, to homologize this bone with the supratemporal of the Stegocephali or with that of fishes, is not apparent. Thyng calls it the supratemporal, and hence definitely homologizes it with the similarly named bone of his descriptions of the Stegocephali, which has the position of the pterotic of fishes. Williston ('04) proposes for it the name 'paroccipital plate,' and definitely homologizes it with the epiotic (tabulare) of the Stegocephali, It, however, seems to me to certainly be the dermopterotic of fishes, and it certainly does not include the dermo-

sphenotic. Ventral to it there is another bone, which Gaupp first called the paraquadratum but later the squamosal. Thyng calls it the squamosal, and hence homologizes it with that bone of his descriptions of the Stegocephali, which is the cheek-plate of fishes. Williston calls it the squamosal, but the so-named bone of the terminology at that time employed by him lies dorsal to the cheek-plate and hence in the position of the pterotic of fishes. The hind end of this bone lies, in early embryos, ventral to the bone above referred to as the dermopterotic, and external to the dorsal end of the quadrate, but in the adult it has shifted upward on to the external surface of the dermopterotic. From there the bone extends anteriorly, or anteroventrally, and is applied along the ventral edge of the postorbital, there approaching but not quite reaching the hind end of the jugal. In Lacerta there are two postorbital bones, the dorsal one called by Gaupp the postfrontal. In Scleroporus these two bones have fused to form a single postorbital.

Comparing the conditions in these two saurians with those in Hatteria and fishes, it seems certain, as above stated, that the dorsoposterior one of the two bones here under consideration is the dermopterotic. A dermosphenotic is then wanting, unless it be represented in the so-called squamosal of the authors quoted. The position of the latter bone in early embryos, and its later position along the ventral edge of the postorbital, are, however, opposed to this view, and it seems probable that the dermosphenotic does not develop, possibly being represented in the cord of tissue said by Gaupp ('00; p. 463) to extend, in Lacerta, from the tip of the processus paroticus to a sharp ridge which runs forward dorsal to the columella auris. The dermosphenotic not being present, the temporal arch of these reptiles is formed by the cheek-plate and postorbital of fishes, and corresponds to that part of the inferior temporal arch of Hattaria that is formed by the ventral process of the squamosal of that reptile. The small fenestra said by Williston ('04; p. 183) to have been figured in one species of Cyngonathus, but disputed by Broom, might then be a fenestra between this arch of the Sauria and the infratemporal arch of Crocodilus.

There thus apparently are four distinctly different temporal arches in the vertebrates above considered: one formed by the dermosphenotic and the postorbital (man, upper arch in Hatteria and Crocodilus); one formed by the cheek-plate of fishes and the postorbital or jugal (Lacerta, Scleroporus, part of lower arch of Hatteria); one formed by the quadratojugal and jugal (lower arch of Crocodilus, part of lower arch of Hatteria), and one formed by the quadratojugal and maxillary (Amphibia).

Palais de Carnolès, Menton,
June 22, 1919

LITERATURE CITED

Allis, E. P., Jr. 1889 The anatomy and development of the lateral line system in Amia calva. Jour. Morph., vol. 2, no. 3. Boston.

1904 The latero-sensory canals and related bones in fishes. Intern. Monatsschr. f. Anat. u. Physiol., Bd. 21, Leipzig.

1918 On the origin of the hyomandibula of the Teleostomi. Anat. Rec., vol. 15. Philadelphia.

(In press) On the homologies of the auditory ossicles and the chorda tympani.

(In press) On certain features of the otic region of the chondrocranium of Lepidosteus, and comparison with other fishes and higher vertebrates.

Bryce, T. H. 1915 Osteology and arthrology. Quain's Anatomy, 11th edition. vol. 4, pt. 1. London.

Fuchs, H. 1910 Betrachtungen über die Schläfengegend am Schädel der Quadrupeda. Anat. Anz., Bd. 35.

1911 Über die Beziehungen zwischen den Theromorphen Cope's bezw. den Therapsiden Broom's und den Säugethieren (etc). Zeit. Morph. Anthrop., Bd. 14. Stuttgart.

Gaupp, E. 1894 Zur vergleichenden Anatomie der Schläfengegend am knöchernen Wirbeltheier-Schädel. Morph. Arb. v. G. Schwalbe, Bd. 4.

1900 Das Chondrocranium von Lacerta agilis. Ein Beitrag zum Verständnis des Amniotenschädels. Anat. Hefte, Bd. 14.

1910 Säugerpterygoid und Echidnapterygoid nebst Bemerkungen über das Säuger-Palatinum und den Processus basipterygoideus. Anat. Hefte., Bd. 42.

Goodrich, E. S. 1919 Restorations of the head of Osteolepis. Journ. Linn. Soc.: Zoology, vol. 34. London.

Gregory, W. K. 1917 Second report of the committee on the nomenclature of the cranial elements in the Permian Tetrapoda. Bull. Geol. Soc. Amer., vol. 28.

Kunkel, B. W. 1911 Zur Entwickelungsgeschichte und vergleichenden Morphologie des Schildkrötenschädels. Anat. Anz., Bd. 39.

MOODIE, R. L. 1908 The lateral line system in extinct Amphibia. Jour. Morph., vol. 19.

POLLARD, H. B. 1892 On the anatomy and phylogenetic position of Polypterus. Zool Jahrb., Bd. 5.

SCHAUINSLAND, H. 1903 Beiträge zur Entwicklungsgeschichte und Anatomie der Wirbeltiere, 1, 2, 3, Zoologica, Bd. 16.

SHIINO, K. 1914 Studien zur Kenntnis des Wirbeltierkopfes. 1. Das Chondrocranium von Crocodilus mit Berücksichtigung der Gehirnnerven und der Kopfgefässe. Anat. Hefte, Bd. 50.

THYNG, E. W. 1906 Squamosal bone in tetrapodous Vertebrata. Proc. Boston Soc. N. R., vol. 32.

TRAQUAIR, R. H. 1876 On the cranial osteology of Polypterus. Journ. Anat. Physiol., ser. 2, no. 7.

1877 Ganoid fishes of the British Carboniferous formations. 1. Palaeoniscidae. London.

1881. VII. On the cranial osteology of Rhizodopsis. Trans. Royal Soc. Edin., vol. 30, pt. 1.

WATSON, D. M. S., AND DAY, H. 1916 Notes on some Paleozoic fishes. Memoir Manchester Literary and Philos. Soc., Sess. 1915–1916.

WIJHE, J. W. VAN 1882 Über das Visceralskelet und die Nerven des Kopfes der Ganoiden und von Ceratodus. Niederl. Archiv f. Zool., Bd. 5.

WILLISTON, S. W. 1904 The temporal arches of the Reptilia. Biol. Bull. Woods Hole, vol. 7.

Resumen por el autor, Augustus G. Pohlman.
Universidad de San Luis.

Sobre el factor que causa la salida del huevo en el pollo, con especial referencia al músculo complejo.

El autor representa en dos tablas la comparación del análisis del peso del músculo complejo en estado fresco y después de seco, las cuales indican la existencia de una marcada infiltración linfática antes y en el momento de romper el pollo la cáscara del huevo. Los resultados obtenidos en una serie de 80 pollos, de edad variable entre los 19 dias de incubación hasta el octavo dia después de salir del huevo, indican que el músculo complejo sufre una atrofia después de abandonar el pollo el cascarón, la cual debe explicarse mediante un estudio comparativo. La infiltración linfática se debe a la rápida absorción de la porción liquida de la yema en el momento en que el saco vitelino penetra dentro del cuerpo del pollo, y en parte también a la naciente actividad glandular. El liquido se acumula en el cuerpo hasta después de abandonar el huevo el animal, porque la principal ruta para la excreción del agua es a través de los pulmones. El autor compara la salida del huevo del pollo con el momento del nacimiento en un mamífero; la penetración del vitelo es comparable a las contracciones del útero y la extensión de la cabeza y vértebras cervicales comparable a los reflejos respiratorios de la madre, que acompañan al acto del parto. El mecanismo de los reflejos en ambos casos se debe a la presión ejercida sobre el músculo elevador del ano. La extensión actual de la cabeza y las vértebras cervicales tiene lugar mediante contracciones de los músculos espinal y biventre y no por el músculo complejo, como supone Keibel.

Translation by José F. Nonidez
Carnegie Institution of Washington

AUTHOR'S ABSTRACT OF THIS PAPER ISSUED
BY THE BIBLIOGRAPHIC SERVICE, OCTOBER 13

CONCERNING THE CAUSAL FACTOR IN THE HATCHING OF THE CHICK, WITH PARTICULAR REFERENCE TO THE MUSCULUS COMPLEXUS

A. G. POHLMAN

Department of Anatomy, St. Louis University

TWO CHARTS

The writer[1] in a brief review, "On the Causes of Birth," called attention to the point that not until the factors which drive the developing chick from the shell have been satisfactorily established are we justified in speculating on the causal factors in the mammal where the relations are complicated by a maternal mechanism. It was also mentioned that the embryo appears to determine its 'ripeness' in terms of altered metabolism. This altered metabolism, which is an elastic term, may be held responsible, directly or indirectly, for the application of the forces necessary to break the barriers and deliver the embryo from its membrane respiration and watery environment into the air as a lung breather. The forces which bring about the delivery of the mammalian embryo are developed wholly by the mother, and the stimulation to uterine contractions, or the release of inhibiting agencies to these contractions, are probably chemically controlled by the embryo, although the suppressed menstrual cyclage of the mother contributes in determining the time. It is interesting to note that with a summation of uterine contractions, additional voluntary musculature is touched off, possibly due in part to the distending forces involving the region of the M. levator ani. The chick, however, presents a different picture, because the hatching involves only its own mechanism. Probably like the mammal, two active forces are at work—a

[1] Pohlman, A. G., On the causes of birth. Johns Hopkins Hospital Bull., vol. 23, Dec., 1912.

contraction of involuntary musculature and as a result of abdominal distention, a second response in voluntary musculature—probably respiratory in character and perhaps dependent on the tension of the M. levator ani. It is the purpose of this paper to deal in particular with the M. complexus of the chick, because to this muscle has been ascribed the function of breaking the shell, and to call attention to certain other anatomical and physiological problems connected with the chick at the time of hatching, which may prove fruitful fields for investigation.

Keibel,[2] in a very brief note, states his views on this question, and the writer not only takes the liberty of translating this article freely, but also assumes, from his past friendly relations as a student with Professor Keibel, that permission to work on this problem would have been freely granted had communication been possible.

When one asks the question—How does the hatching chick break through the shell? The answer which naturally comes to mind is, "by means of its egg-tooth." The egg-tooth and its development has been the subject of repeated investigations recently by R. Rosenstadt; but the egg-tooth and the bill after all are nothing more than the instruments used in breaking the shell. The muscular apparatus which furnishes the power to these instruments affords certain peculiarities in structure which have not hitherto been described. It occurred to me in the course of the investigation of other problems, that the M. complexus in the chick undergoes marked alterations in structure before the hatching and during the period of breaking the shell. The muscle, which is divided into three segments by two Inscriptiones tendineae, becomes greatly hypertrophied and infiltrated with serous fluid. On the tenth day after the hatching, the muscle shows nothing unusual in its structure. It follows, therefore, from what has been said, that the M. complexus is the chief active agent in breaking through the shell. It is well adapted, by reason of its position, to thrust the egg-tooth through the shell. This undoubtedly requires no small amount of force, but in what manner the force becomes operative has not been described. We now know that the M. complexus which functionally hypertrophies at the time of hatching, supplies the chick with the power essential to breaking through the shell. Inasmuch as I have observed the same hypertrophy in the ducklings, it is not unlikely that this arrangement obtains in all birds. Further details on the histological structure of the muscle I reserve for later publication.

[2] Keibel, F. Anatomischer Anzeiger, Bd. 41, 1912.

It would appear at first glance that Keibel's explanation is indeed satisfactory and that it leads us one step nearer to the solution of a perplexing problem, but the most unusual condition of a voluntary muscle undergoing a functional hypertrophy which antedates its function seemed so peculiar, that the writer resolved, in gathering material for the study of the behavior of the double ductus arteriosus system, to investigate the M. complexus in greater detail.

The article by Rosenstadt,[3] while it is a report on the histogenesis of the egg-tooth, presents certain conclusions which Keibel does not mention in his brief preliminary. "It appears that the egg-tooth may be regarded as an embryological structure with no particular physiological significance. I have never been able to convince myself that it plays a part in the actual hatching of the chick and must, therefore, consider it a rudimentary organ. It is possible that the egg-tooth is a phylogenetically older organ which, for a time, formed the only weapon (Bewaffnung) with which the jaw was provided."

METHOD USED

Inasmuch as Professor Keibel has reserved the histological side of the investigation of the problem, it was necessary to select some other method, particularly one which would give greater latitude in the study of large amounts of material, and because of the inaccuracies in histological technique. These inaccuracies consist in the great difficulty of obtaining exact cross-sections midway between the tendinous intersections; second, in the unavoidable shrinkage even under the most painstaking histological procedure; third, because of the great individual variability in the muscle itself, and, lastly, because it is impossible to determine within twelve hours to twenty-four hours the exact period of incubation.

The M. complexus of both sides were carefully dissected out; weighed; dried in a desiccator over sulphuric acid for three days and again weighed. The idea being to ascertain if the per cent

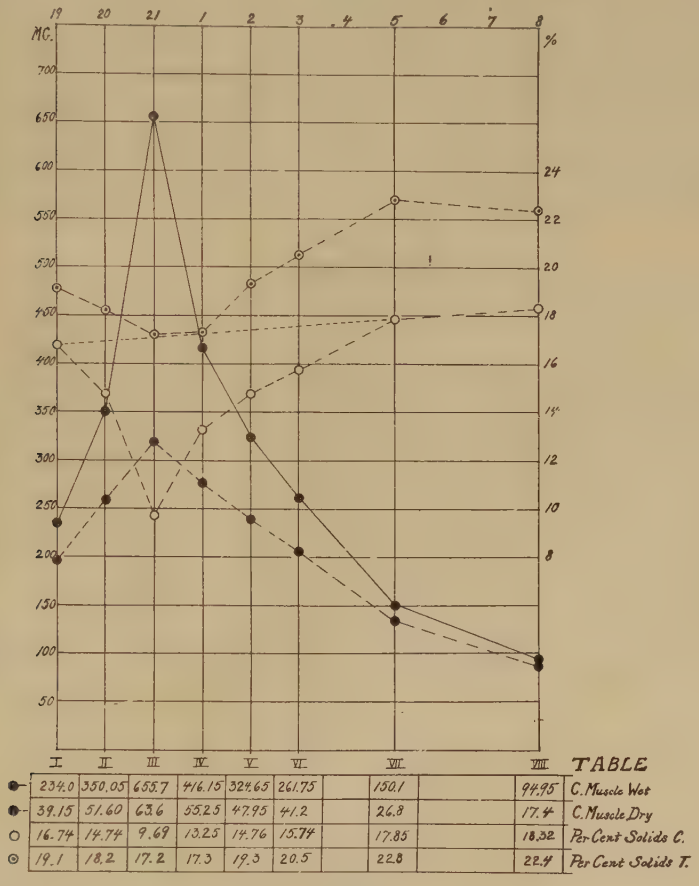
[3] Rosenstadt. Arch. f. mikro. Anat., 1912.

of solids would furnish a clue as to what actually occurred in the muscle mass. The experiments were checked by a bit of pectoral muscle from the same birds. The results obtained by this method were so surprising that the second run of experiments was undertaken in a series of ten chicks—representing roughly the 19th, 20th, and 21st day of incubation and 1st, 2nd, 3rd, 5th, and 8th day after hatching. The same technique was used, excepting the chicks were all killed with ether vapor and the muscles immediately dissected out and weighed. Instead of taking pectoral muscles as a check, it was thought desirable to select one from a more remote region, and a piece of flexor of thigh was removed and treated in the same way. The results are shown in tables 1, 2, 3, 4, 5, 6, 7, and 8. All eggs or chicks were taken at random, from the same incubating brood of Rhode Island Reds, with the exception of stage III, where only eggs in which the shell was picked were selected. The tables show the date and number of the egg or chick in column 1; 2, the weight of the egg or chick in grams; 3, the weight of both complexus muscles when taken from the bird; 4, the weight of the same specimen dried, in milligrams; 5, the percentage of solids obtained by dividing the wet weight into the dried weight; 6, the weight of the segment of flexor of thigh wet; 7, the same segment dried, and 8, the per cent of solids. No effort was made to shunt chicks from one group to the other and with the exception of table 3, 22-IV thigh in which there is an obvious error, all averages are based on the ten specimens in each group.

Great care was used in eliminating all fats, and that this error was fairly well avoided is shown in a 3.9 per cent content as determined by ether extraction of the ground dried specimens. The interesting figures in these tables are shown graphically in chart 1, which has been built up of four averages: the weight of the complexus muscles wet in milligrams; 2, the weight of the complexus muscles dried (figures in milligrams and curve in milligrams times 5); 3, the per cent of solids in the complexus, and, 4, the per cent of solids in the thigh muscle.

It will be noted in following the curve for the average weight of the paired wet complexus muscles, that it rises sharply from

stage I (19th day) to stage III (21st or 'picker' day), and that it also declines rapidly, taking roughly three days to lose what it gained in two; falling off more slowly, so that on the eighth day after hatching the muscles actually weigh less than one-half of



TABLE

I	II	III	IV	V	VI	VII	VIII	
234.0	350.05	655.7	416.15	324.65	261.75	150.1	94.95	C. Muscle Wet
39.15	51.60	63.6	55.25	47.95	41.2	26.8	17.4	C. Muscle Dry
16.74	14.74	9.69	13.25	14.76	15.74	17.85	18.32	Per Cent Solids C.
19.1	18.2	17.2	17.3	19.3	20.5	22.8	22.4	Per Cent Solids T.

CHART 1

what they weighed two days before hatching. The curve of maximum and minimum weight for each stage follows the average very closely. Following the curve for the average dried weight (which curve is exaggerated times five) the marked rise in stage III and the marked fall in stage IV of the fresh muscles

TABLE 1

June 20, 1919

1	2	3	4	5	6	7	8
20. I	47.7	224.0	32.0	14.3	260.0	46.0	17.6
20. II	59.7	302.0	48.0	15.8	234.0	41.5	17.7
20. III	45.5	161.0	32.5	20.1	186.0	30.5	16.3
20. IV	50.5	220.0	33.0	15.0	181.0	37.0	20.4
20. V	57.8	328.0	53.0	16.1	254.0	53.0	20.8
20. VI	55.5	264.0	39.0	14.7	264.0	49.5	18.7
20. VII	51.5	220.0	41.5	18.8	198.0	38.5	19.4
20. VIII	46.6	186.0	39.5	21.2	221.0	45.0	20.3
20. IX	52.2	228.0	33.0	14.4	196.0	36.0	18.3
20. X	45.5	207.0	40.0	19.3	185.0	41.0	22.1
Average	51.25	234.0	39.15	16.74	217.9	41.8	19.1

TABLE 2

June 21, 1919

1	2	3	4	5	6	7	8
21. I	44.0	219.0	36.0	16.4	189.0	35.5	18.7
21. II	54.5	440.0	66.5	15.1	217.0	38.0	17.5
21. III	47.0	349.5	49.0	14.0	152.0	30.0	19.7
21. IV	49.5	350.0	45.0	12.8	188.0	33.5	17.7
21. V	60.5	402.0	51.5	12.8	240.0	40.5	16.9
21. VI	48.5	240.5	47.0	19.5	181.0	37.0	20.4
21. VII	63.0	342.5	56.5	16.4	179.5	32.5	18.1
21. VIII	46.0	275.0	45.5	16.5	137.0	25.5	18.6
21. IX	51.5	436.0	60.0	13.7	208.0	37.5	18.0
21. X	50.5	446.0	59.0	13.2	314.0	55.5	17.6
Average	51.50	350.05	51.60	14.74	200.55	36.55	18.2

TABLE 3

June 22, 1919

1	2	3	4	5	6	7	8
22. I	44.5	557.0	55.5	9.9	272.0	50.0	18.3
22. II	43.5	537.0	65.5	12.1	240.0	44.5	18.5
22. III	39.5	641.5	58.0	9.0	183.0	34.0	18.5
22. IV	44.5	642.0	67.0	10.4	180.5[1]	22.0[1]	12.1[1]
22. V	44.5	710.5	65.0	9.1	310.5	43.5	14.0
22. VI	46.5	951.0	82.5	8.6	212.0	33.0	15.5
22. VII	41.0	552.0	61.5	11.1	185.0	33.5	18.1
22. VIII	60.5	727.0	67.0	9.1	267.5	41.5	15.5
22. IX	44.5	690.5	58.0	8.3	261.0	45.0	17.2
22. X	44.5	548.5	56.0	10.2	191.5	41.5	21.6
Average	45.5	655.7	63.6	9.69	235.8	40.7	17.

[1] Eliminated because of error.

TABLE 4

June 23, 1919

1	2	3	4	5	6	7	8
23. I	41.0	482.0	47.0	9.7	197.0	28.5	14.4
23. II	38.0	432.0	53.0	12.2	276.5	51.5	18.6
23. III	38.0	324.5	49.5	15.2	218.0	32.0	14.6
23. IV	32.0	373.0	45.0	12.0	305.5	61.5	20.1
23. V	39.0	419.5	65.5	15.6	301.0	57.0	18.9
23. VI	35.5	392.0	49.0	12.5	193.0	30.0	15.5
23. VII	36.0	319.0	49.0	15.3	215.5	37.5	17.4
23. VIII	38.0	364.0	54.0	14.8	239.0	40.0	16.7
23. IX	45.0	461.5	57.0	12.3	370.0	62.0	16.7
23. X	40.0	594.0	83.5	14.0	345.5	61.0	17.6
Average	38.25	416.15	55.25	13.25	266.1	46.1	17.3

TABLE 5

June 24, 1919

1	2	3	4	5	6	7	8
24. I	43.5	362.5	52.0	14.3	247.5	43.5	17.9
24. II	38.5	329.0	48.0	14.5	178.5	34.0	19.0
24. III	40.0	350.5	48.0	13.6	301.5	58.5	19.4
24. IV	35.0	393.0	52.0	13.2	173.5	33.5	19.3
24. V	35.0	390.5	57.5	14.7	193.5	40.0	20.6
24. VI	34.0	304.5	46.0	15.1	209.5	41.0	19.5
24. VII	28.0	290.5	47.5	16.3	180.5	37.5	20.7
24. VIII	40.0	297.0	48.0	16.1	213.0	40.5	19.0
24. IX	38.0	266.5	42.5	15.9	197.5	37.5	18.9
24. X	40.0	262.5	38.0	14.4	238.0	46.0	19.3
Average	37.2	324.65	47.95	14.76	213.3	41.20	19.3

TABLE 6

June 25, 1919

1	2	3	4	5	6	7	8
25. I	32.0	152.0	28.0	18.4	139.0	33.0	23.7
25. II	33.0	392.0	62.5	15.9	191.5	35.5	18.5
25. III	33.5	285.5	38.5	13.4	198.5	39.5	19.8
25. IV	36.0	182.0	30.5	16.7	129.5	28.0	21.6
25. V	40.0	251.0	40.0	15.9	170.5	33.0	19.3
25. VI	34.0	339.0	48.0	14.1	174.0	36.5	20.9
25. VII	28.5	193.0	31.0	16.0	143.5	30.0	20.9
25. VIII	35.0	279.0	49.0	17.5	155.0	32.5	20.9
25. IX	30.0	289.5	47.0	16.2	168.5	34.5	20.4
25. X	42.0	254.5	37.5	14.7	174.0	36.0	20.6
Average	34.4	261.75	41.2	15.74	164.4	33.85	20.5

TABLE 7

June 27, 1919

1	2	3	4	5	6	7	8
27. I	38.0	201.5	31.0	15.3	124.0	24.5	19.7
27. II	38.0	138.5	23.0	16.6	150.0	36.5	24.3
27. III	45.0	173.0	29.0	16.7	136.0	31.0	22.7
27. IV	42.0	160.5	28.5	17.7	119.5	25.0	20.9
27. V	37.0	105.0	20.0	19.0	135.5	35.0	25.8
27. VI	33.0	124.5	25.5	20.4	101.0	24.5	24.2
27. VII	30.0	98.0	18.5	18.8	121.5	27.0	22.2
27. VIII	35.0	167.5	28.5	17.0	164.5	37.5	22.7
27. IX	37.0	87.5	18.0	20.5	130.5	32.5	24.9
27. X	47.0	245.0	46.0	18.7	193.5	42.0	21.7
Average	38.2	150.1	26.8	17.85	137.6	31.55	22.8

TABLE 8

June 30, 1919

1	2	3	4	5	6	7	8
30. I	32.0	94.5	17.0	17.9	69.5	17.0	24.4
30. II	39.0	108.0	17.0	15.7	81.0	16.5	20.3
30. III	37.0	132.0	18.0	13.6	126.0	23.5	18.6
30. IV	36.0	87.0	18.0	20.6	127.0	28.5	22.4
30. V	35.0	80.0	15.5	19.3	147.0	37.0	25.1
30. VI	35.0	63.5	13.0	20.4	91.5	21.0	22.9
30. VII	38.0	124.5	24.0	19.2	127.0	30.5	24.0
30. VIII	36.0	86.5	18.5	21.3	116.5	26.0	22.3
30. IX	32.0	93.0	18.5	19.8	101.5	22.0	21.6
30. X	30.0	80.5	14.5	18.0	126.0	27.5	21.8
Average	35.0	94.95	17.4	18.32	111.30	24.95	22.4

are wanting. This is explained by following the per cent of solid curve for the complexus. The marked gain in weight is accompanied by an almost equally marked loss in per cent of solids, and the loss of weight is accompanied by an increase in solids. The interpretation lies in the fact that the muscle is infiltrated with a fluid of low solid content. It will be seen on comparing the per cent curve of the complexus with that of the thigh muscle per cent, that while not so marked in the latter,

the dilution of muscle to the stage III and its gradual rise in total solids after the 'picker' stage is easily observed.

The serous material which infiltrates the tissues of the chick on the 19th, 20th, and 21st days is a light orange-colored fluid which impregnates loose connective tissue to the point of making it gelatinous. Some bits of this infiltrated tissue in the 'picker' stage were removed and the solid content was found to be but 4 per cent. This necessarily included a minute amount of fibrous tissue and arbitrarily the solid content was figured at 3.5 per cent.

A second observation of the percentage curve for the complexus showed that when a line is drawn from 16.74 per cent in stage I to 17.85 per cent in stage VII, this line continues to 18.32 per cent in stage VIII (shown in chart 1 as a dotted line). It may be, therefore, that the gradual increase in solids of the muscle is being masked by the infiltration of the low solid content fluid. It was determined to calculate the value of the muscle wet and dried at its probable solid percentage for stages II, III, IV, V, and VI and also to separate the amount of infiltrating fluid and its probable solid content of 3.5 per cent. The estimated solid content of the muscle in per cent is based on the dotted line (chart 1), here shown as an unbroken line at the top of the chart 2.

If a known amount of a mixed fluid, in which the solid content percentage has been determined, is composed of two known fluids, one of greater and one of less solid content, then it is simple to compute how much of each of these two components was present. If the known quantity of fluid is 1, then the two parts are

X and (1 minus X)

Solving this equation for stage II; one material has 16.8985 per cent of solids, the other 3.5 per cent of solids; 350.05 milligrams show 14.74 per cent of solids. Therefore, the: X plus (1 minus X) = 14.74 per cent

16.8985X plus 3.5 (1 minus X) = 14.74 or
16.8985X plus 3.5 minus 3.5X = 14.74
16.8985X minus 3.5X = 14.74 minus 3.5 or
13.3985X = 11.24 or

$$X = \frac{11.24}{13.3895} \text{ or}$$

$$X = \frac{11.24 \text{ times } 350.05}{13.3985} \text{ or}$$

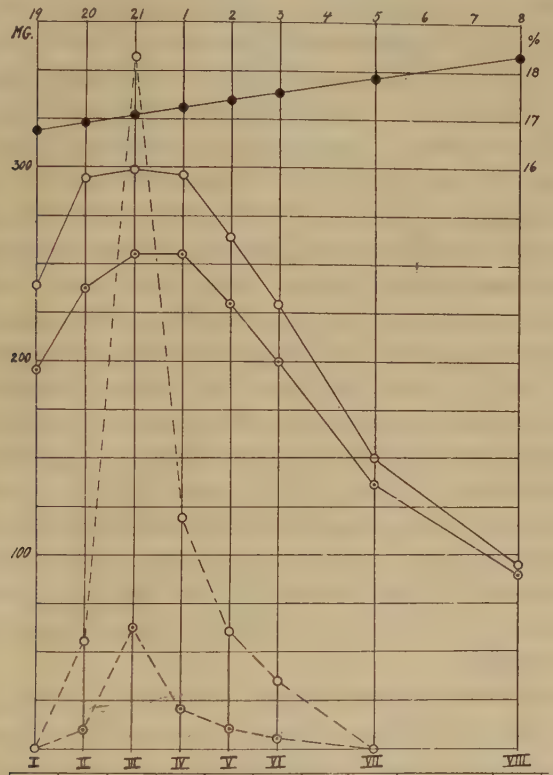
X = 294.0 mg., the calculated amount of muscle before drying, and to gain the dried weight, 294.0 times 16.8985 per cent = 49.68 mg. dried. The other amount = 350.05 minus 294.0-56.05, the amount of lymph in milligrams or times 3.5 per cent is 1.86 mg. dried lymph.

49.68 plus 1.86 = total solids for this stage = 51.54. It should be 51.60, and the small error is due to minute fractions. This done for II, III, IV, V, and VI, it is possible to construct chart 2, in which five variable factors enter: 1, the calculated weight of the paired muscle proper; 2, the calculated amount of lymph; 3, the weight of the solids for the muscle; 4, the weight of the solids for the lymph, and, 5, the estimated solid percentage for muscle.

Analysis of chart 2 shows quite definitely the excessive infiltration of lymph from 56.05 mg. in stage II to 356.4 mg. in stage III; rapidly dropping to 119.75 mg. in stage IV. The calculated muscle, however, rises from 234 to 294 mg. in stage II, then practically maintains this weight for the two successive stages III and IV, and gradually drops off to stage VIII. This is to be interpreted as follows: that the complexus muscle attains its maximum development at the twentieth day of incubation; maintains this maximum through the hatching and first day out; then begins to decrease in size; second, that before the hatching the muscle becomes infiltrated with lymph which attains its maximum at the 'picker' stage, after which the excess of lymph is rapidly lost.

This brings to mind a series of questions: 1. What is the origin of the excess of lymph at this stage of the development? 2.

Why is the complexus muscle more markedly infiltrated than the thigh or pectoral muscles and what effect does this infiltration have upon its function? 3. Why does the muscle undergo a progressive atrophy after hatching?



o—	234.0	294.0	299.3	296.4	263.7	228.2	150.1	94.95	Muscle Estimated
o---	0	56.05	356.4	119.75	60.95	35.55	0	0	Excess Lymph Estimated
	234.0	350.05	655.7	416.15	324.65	261.75	150.1	94.95	Total Wet Weight (Curve I)
⊙—	39.15	49.68	51.05	51.02	45.81	40.02	26.8	17.4	Muscle Dry Estimated
⊙---	0	1.86	12.47	4.19	2.13	1.17	0	0	Lymph Dry Estimated (3.5%)
	39.15	51.60	63.6	55.25	47.95	41.2	26.8	17.4	Total Dry Weight (Curve I)
●—	16.74	16.898+	17.057	17.215+	17.374	17.532+	17.85	18.32	Estimated Muscle Solids %

CHART 2

1. The chick apparently is subject to a series of changes some forty-eight hours before it picks the shell. The yolk which lies loosely below its body like a two-winged process on either side of its abdomen becomes gradually injected into the digestive

tract through a contracture of the smooth muscle tissue of the amnion. This is apparently anticipated by decrease in the yolk blood-vessels and is accompanied by an increased oxygen consumption as determined by Preyer,[4] probably indicating glandular activity. The result is a rapid absorption of the fluid part of the yolk and a consequent distention of the vascular system. As the yolk becomes forced more and more into the digestive tract, the blood of the allantoidal system is also taken up into the body vessels. This distention with fluid results in the escape of lymph into the tissues because either the chicks' kidneys are not competent to handle the large amount of fluid or are mechanically interfered with through abdominal pressure, or the chicken's water excretion may take place largely through the lungs. This latter seems most probable and accounts for the ability of the hatched chick to go for three or four days without water; for the rapid falling off in water following the hatching, and for the failure of the new chick to exhibit any pronounced water excretion through the kidneys. The obvious distention of the chicken at the 'picker' stage is not only evident from casual inspection, but may be seen readily on comparing serials of twenty-day chicks and those one day out of the shell. That the transudation of fluid occurs all over the bird is readily observed in curve I, by following the line of percentage solids for the thigh muscle.

2. The M. complexus appears to become more markedly infiltrated with lymph than other muscles because of its structure, its position, and its function. The structure of the muscle, as Keibel has described it, is a true segmented muscle separated into three portions by two tendinous lines. The muscle fibers are practically parallel, loosely bound together with internal perimysium and with no very definite external perimysium on the surface where the connective tissue becomes continuous with the loose subcutaneous tissue. The deep surface of the muscle shows a better developed fascial plane separating it from the underlying muscles which are also infiltrated, but not in so marked a degree.

[4] Preyer. Physiologie des Embryos.

This infiltration also takes place immediately above the attachment of the muscle to the skull and below the muscle origin in the subcutaneous connective tissue of the dorsal cervical region. The infiltration is so pronounced that unless one knew definitely the gelatinous golden-yellow mass was muscle, it would be difficult to recognize it as such. Even the tendinous intersections are practically blotted out in stages II, III, and IV. It would appear, therefore, that this area represents a loose or relaxed subcutaneous region, lying in a position where the infiltrating fluid can readily pass out of the blood-vessels.

The distention of the muscle begins about forty-eight hours before the picking of the shell, and at the time of picking the muscle has its maximum amount of lymph excess. It would appear from what is generally known of muscle function that a marked infiltration of lymph seriously interferes with contraction, and this leads to a somewhat different view from the one expressed by Keibel. The muscle becomes greatly infiltrated partly as a result of its structure, its position, and from the point that it is relaxed at the time of the picking through the shell. This, however, affords no explanation why the muscles atrophy after hatching, nor does it suggest the causal factor in the breaking of the shell.

3. The atrophy of the muscle which is pronounced on the basis of curve II, from 51 mg. for the paired muscle at the time of hatching to 17.4 mg. in the eight-day chick, is so pronounced, in spite of the loading with high solid content material within the fibre, that it may readily be seen both in gross inspection and in sections. In addition, the muscle insertion into the occipital region shifts lateralward, so that the underlying M. biventer begins to come to a surface position. This implies in a general way that the chick's M. complexus is too large for its later uses and the analysis of why this obtains must be determined by study of birds with large heavy bills; where the head balance and particularly rotation of the head involves much muscular effort (pelican) or in birds capable of sustaining great weights from their bils (eagle). The answer must come from a comparative study.

The causal factor in breaking the shell at the present writing is not absolutely clear, excepting in the fact that the head position shifts from the normal egg position of flexed lateral rotation to one of extension with the head carried more nearly on the vertebral axis.[5] The extension of the vertebrae at the lower cervical region is easily as pronounced as the infiltration of the M. complexus, and is mainly due to the M. spinalis and M. biventer. It is, therefore, not unlikely that the chief agent in extending the neck and through progressive attachment maintaining a somewhat extended head is a function of this muscle system. The call for this action after the hatching would increase progressively, and correspondingly the M. spinalis and M. biventer undergo hypertrophy. The muscle mass may be divided into three portions and may be checked up in the same manner as the M. complexus.

Even if we grant that extension of the neck and placing the head on a line with the general vertebral axis are more or less the direct power factor which has to do with the breaking of the shell, the origin of the reflex mechanism which brings about this action is still hidden. It may be due to a beginning functional sense of equilibrium which is fairly well developed in the newly hatched chick or it may be a respiratory-choking reflex brought about by an abdominal distention and a pressure against the M. levator ani, which in the bird is a distinct respiratory muscle. The reflex mechanism of distending the levator ani region is familiar even in the human being in its association with respiration—during defecation, during parturition, and through anal dilatation in artificial respiration. The demand for oxygen can hardly be called a major factor because, granting a gradual decrease in allantoidal respiration and even granting an increased demand for oxygen due to glandular activity or for the maintenance of body heat, the onset would be so gradual that a distinct respiratory reflex would be improbable. It seems, after all, that what is found in the delivery of the mammalian embryo by the mother finds a somewhat similar mechanism in the birds. The injection of the yolk sac being comparable to the uterine

[5] Lillie. The development of the chick.

contraction, and the result of the abdominal pressure either mechanically or in summation of the involuntary muscular stimulation involving a respiratory reflex in the mammal which brings additional forces to bear on the parturient act, and in the bird brings about the drinking-choking reflex which results in marked extension of the upper cervical vertebrae.

It would appear, from the few observations made, that the breaking of the shell is a result of a pressure rather than a sudden muscular effort, and this pressure might readily come about from the change in neck positions and from the build of the egg-tooth which tends to slip up the side of the dome of the shell readily, but is not so easily displaced downward.

In review, it would appear that Professor Keibel's contention that the M. complexus is the chief active agent in breaking the shell is open to serious objection.

1. The muscle attains a maximum development before and at the stage of hatching, and a progressive atrophy after the chick is hatched at least up to the eighth day.

2. Before the time of hatching, the M. complexus becomes infiltrated with lymph which attains its maximum with the complete injection of the yolk and the discharge of the allantoidal blood into the systemic vessels.

3. The infiltrated muscle is physiologically incapacitated to undergo pronounced muscular contraction, and one reason for the marked infiltration is undoubtedly due to its relaxed condition.

4. The active muscular agent in breaking the shell comes about through a change in posture of the head and upper cervical vertebrae chiefly dependent on the M. biventer and M. spinalis.

5. The reflex mechanism which touches off this muscle system is probably a respiratory reflex, not dependent on demand for oxygen, but dependent on distention of the abdomen, particularly the M. levator ani, brought about through injection of the yolk sac.

6. The enormous lymph infiltration is a result of rapid absorption, partly due to pressure and partly due to awakened glandular activity as positive factors, and to the failure of the kidneys, either due to pressure or failure of this gland to take care of the excess of water in birds, as negative factors.

7. Not until respiration sets in does the general edema disappear, which implies that most of the water in birds is excreted by the lungs, and also accounts for the ability of the new-born chick to go at least three days and perhaps four and even five days without water.

A SIMPLE MOUNTING FOR DEMONSTRATION SLIDES

RICHARD E. SCAMMON

Institute of Anatomy, University of Minnesota

ONE FIGURE

The mounting and preservation of special and demonstration slides is sometimes a matter of considerable importance, particularly when the specimens are not easily duplicated. For the past year the mounting device shown in the figure below has been in use in this laboratory, and it has proved so useful that its description has seemed worth record.

The mounting consists of a card 3 by 5 inches—the size used in most cataloguing work. It is made of heavy white cardboard, approximately 2 mm. thick. In the center of this card is cut a rectangular opening, 26 by 76 mm., which will just accommodate an ordinary slide. The slide to be mounted is placed in the opening and strips of passe-partout paper, three-eighths of an inch in width, are pasted along its upper and lower edges and to the adjacent edges of the card. These strips are cut long enough so that they extend a little beyond the ends of the slide to the right and left. They are pasted on both the front and back surfaces of the card. Two more strips of passe-partout paper, cut to the proper length, are then pasted completely around the card from front to back in such a position that they will cover the ends of the slide and also the cut ends of the horizontal strips of paper which hold the upper and lower edges of the slide in place. In this way the slide is bound in position within the opening and is held securely along all of its edges.

Slides mounted in this way may be filed in ordinary card-catalogue boxes and occupy but little space. The unoccupied portion of the card affords considerable space for a record of the specimen.

Mounts of this kind are practically unbreakable in ordinary class use and, so far as our experience goes, they do not warp or crack. The cost of a single mount, including the price of the original die for cutting the slit in the card, is about two cents.

A device somewhat similar to the present one was recently described by Robinson.[1] He uses a somewhat larger card with

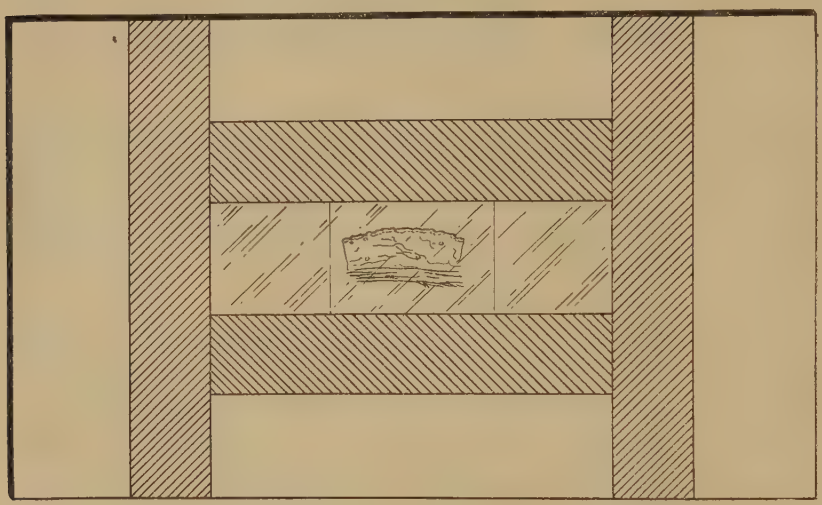


Figure 1

a circular opening cut through the lower part. The slide is fastened to the back of the card behind the opening. This mounting has the advantage of allowing more space on the card for a record, and is therefore particularly useful for autopsy material, but the mounting is not as secure as the one here described nor do the cards file so compactly.

[1] A convenient method for filing surgical sections. Jour. Am. Med. Ass., vol. 71, pp. 1379, 1380.

A CASE OF THORACIC STOMACH[1]

PERCIVAL BAILEY

Anatomical Laboratory of Northwestern University Medical School

TWO FIGURES

There have been many cases reported of hernia of the stomach into the thorax, but so far as I can find in the literature, no actual case of development of the stomach in the thorax. Such a case I wish to report.

The condition was found in the course of the regular dissection. The body was that of a certain Ephraim Trimble, who died in the Lake Forest Sanitarium of Cook County, at the age of seventy-seven. In his clinical history there was, strange to say, no mention of any gastric disturbance, and the nurse in charge of his ward stated that his appetite was good to within a short time of his death and that he never complained of any trouble referable to his stomach. Neither were there any discoverable cardiac disturbances. Clinically, there was no reason to suspect any abnormality. He died of arteriosclerosis and interstitial nephritis.

On opening the abdomen, it was found that only the pyloric antrum was present in the abdominal cavity, projecting downward a distance of 6 cm. (fig. 1). At the opening in the diaphragm, the diameter of the stomach was about 2 cm. The duodenum was of course practically completely visible, only the lowest part being covered by the transverse mesocolon. For a distance of 10 cm. beyond the pyloric sphincter it was bound to the liver by the lesser omentum. The rest of the duodenum not covered by the transverse mesocolon was attached only by the dorsal meso, resembling in shape very much the sigmoid mesocolon, an unusual case of persistence of the dorsal mesoduodenum.

[1] Contribution no. 75.

The opening in the diaphragm lay at the level of the eleventh thoracic vertebra. It was 4 cm. in width. The anterior border was formed by a tough fibrous band which was attached at either end to the body of the eleventh thoracic vertebra and hugged the vertebra closely so that the opening was a semicircular slit. Through it the abdominal cavity communicated freely with a cavity in the thorax.

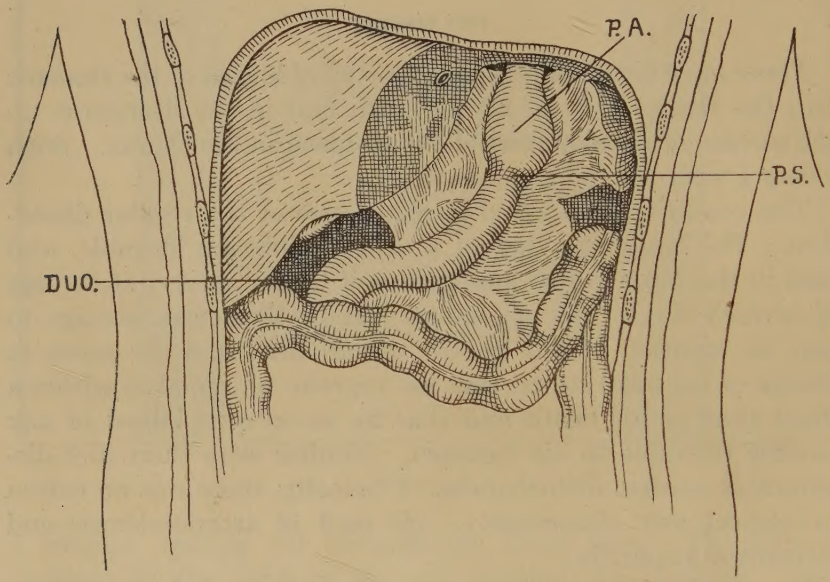


Fig. 1 Anterior view of upper part of abdomen. The left lobe of the liver has been removed. *P.A.*, pyloric antrum; *P.S.*, pyloric sphincter; *DUO.*, duodenum.

On opening the thorax, the body of the stomach was found to lie between the pleural cavities and behind the pericardium, in the posterior mediastinum. It was completely surrounded by a serous sac which was continuous with the peritoneum through the opening in the diaphragm. (Fig. 2). There was a rudimentary greater omentum. The left gastric artery arose from the coeliac and the left gastroepiploic from the splenic at the usual level and passed upward through the diaphragm to the stomach.

The oesophagus was straight and ended at the level of the third costal cartilage.

It will be seen from this brief description that there is no evidence that the stomach had herniated into the thorax. Its position and relations may be explained by supposing that the anlage of the stomach lay abnormally far anterior on the ali-

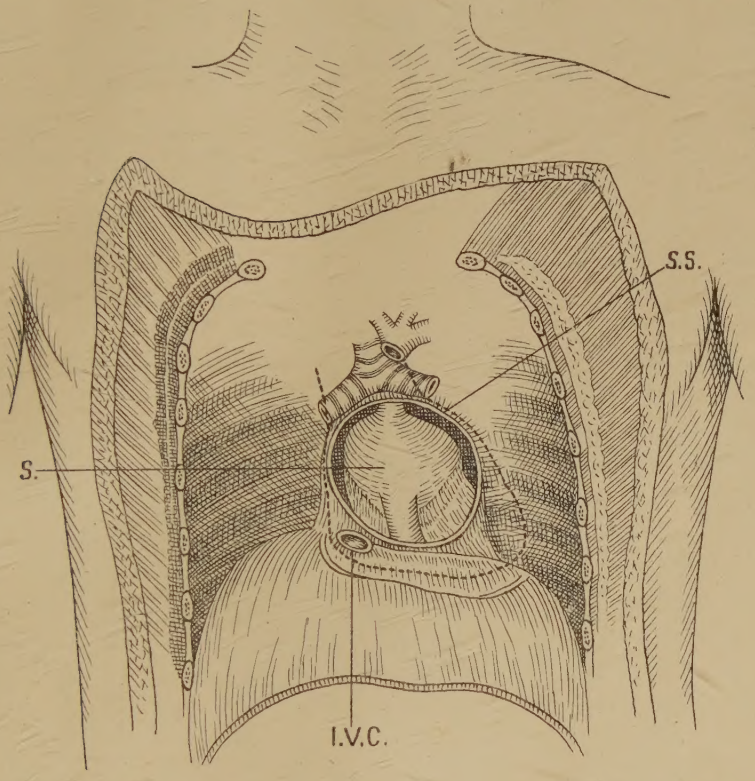


Fig. 2 Anterior view of thorax. Lungs and heart removed and serous sac surrounding stomach opened. Position of heart indicated by dotted lines. *S.*, stomach; *S.S.*, serous sac around stomach; *I.V.C.*, inferior vena cava.

mentary canal. The peritoneal pockets around the stomach develop before the descent of the diaphragm, and finding the peritoneal relations already developed, the diaphragm would necessarily leave above it, as it descended, not only the stomach, but also the extension of the peritoneal cavity.